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REPRODUCTION OF THE SAND WASPS *STICTIA SIGNATA* (L.) AND *BICYRTES VARIEGATA* (OLIVIER) (HYMENOPTERA: SPHECIDAE) ON THE CARIBBEAN COAST OF QUINTANA ROO, MÉXICO

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Abstract.—Reproductive behavior of the sand wasps *Stictia signata* (L.) and *Bicyrtes variegata* (Olivier) was studied from 1984 to 1988 on the Caribbean shoreline of the Yucatán Peninsula, México. Data on seasonal and diel activity patterns, on prey, and on excavation, orientation, and dimensions of burrows are presented. A male flight polymorphism, previously undescribed for the species, occurred in *S. signata*; some males hovered in flight at various heights near foliage, while others patrolled in sinuous flight near the surface of the beach. Burrows of *B. variegata,* reported from other locations as polycellular, were with one exception unicellular. Characteristics of *B. variegata* at our research site are discussed speculatively as possible consequences of drought.

Key Words.—Insecta, Hymenoptera, Sphecidae, *Stictia signata, Bicyrtes variegata,* reproduction, male flight polymorphism, México

The accumulation of observations on sand wasps has permitted syntheses of hypotheses on their behavioral evolution (Evans 1966, Alcock et al. 1978, O'Neill & Evans 1988). Comparisons between populations of single species from diverse areas and climates have increased the knowledge of behavioral variability that is necessary to understand differences between higher taxa, as well as behavioral plasticity within single demes (Alcock 1979; O'Neill 1983; O'Neill & Evans 1983a, b, 1988).

Stictia signata (L.) and *Bicyrtes variegata* (Olivier) have extensive Neotropical distributions (Evans 1966); aspects of the reproduction of each have been reported from widely separated locations (Janvier 1928, Callan 1954, Vesey-Fitzgerald 1956, Evans 1966, Post 1981, Philippi & Eberhard 1986). Here we describe reproductive patterns of populations of these species that nest on the Caribbean beaches of Quintana Roo, México. We report several behavioral attributes that differ markedly from those previously described for these species, including male flight polymorphism in *S. signata,* and speculate on the role of unusual environmental conditions in influencing behavior.

Methods

Site Description.—We observed wasp behavior on beaches at Akumal (20°24′ N, 87°18′ W), Quintana Roo, México, where sandy embayments alternate with low rocky headlands. Variation in water level at the shore appeared to be more a function of easterly trade wind velocity and direction than of minor semidiurnal tidal changes (< 0.3 m, see Randall & Martin 1987) at the location. Thick vegetation began 100+ m inland. Seasonally flooded dry areas alternated with nearly permanent swampy areas along the coast. The general area was transitional vegetationally, and farther inland on slightly higher ground, elements of deciduous dry forest and rainforest occurred. Development of rural communities with tourist facilities (as at Akumal) presently is common in beachfront areas.

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The year during which our primary data were taken (1985) was one of severe local drought. Rains fell only occasionally and lightly at Akumal before and during our work. This scarcity of rainfall interacted with a series of new and older causeways (impassable to drainage from adjacent areas that received rain) to allow a considerable portion of the normally swampy area inland to become dry and partially devegetated.

Methods.—We did not attempt to investigate all aspects of reproductive behavior equally, but arbitrarily concentrated our effort in areas we deemed most significant and/or time effective. Thus, some behaviors are described in outline, qualitatively, or only by reference to patterns described for the species in the literature. When appropriate we present only ranges of behavior in such descriptions and for those based partly on observations begun or terminated in mid-behavior.

Our observations occurred from dawn to dusk until we were able to discern the outlines of major activity patterns; we then concentrated our efforts over shorter time periods. Observations occurred: 18 Dec 1984; 26–30 Apr, 5 Jun–10 Jul, and 6–15 Aug 1985; 22–27 Apr, 1–7 Jun, 26 Jun–5 Jul, and 20 Dec 1986; 7–18 Jun 1987; and 18 Mar 1988, for a total of 270 h. Data taken during June and July 1985 (190 h) form the bases of most qualitative descriptions, and all those presented in Tables 1 and 2.

Descriptions of male behavior are based on 74 observations of *S. signata*; those of female behavior, primarily on repeated observations at marked burrows of 26 *S. signata* and 30 *B. variegata.* We dug out burrows at which we had previously observed repeated activity (26 of *S. signata,* 30 of *B. variegata*), and we provide statistical data (Table 1) for those at which we had previously observed provisioning and/or which contained provisions.

Wasps were disturbed only occasionally by us during observation and did not appear to be confused (after brief reorientation flights) by the numbered beverage bottle caps that we introduced as burrow markers while the wasps were underground.

Identifications were provided by Arnold Menke and James Gillaspy (sphecids), T. J. Henry (hemipterans), and N. E. Woodley (dipterans).

BIOLOGY

At Akumal, *S. signata* and *B. variegata* aggregated most densely on moderately compacted sand proximate to human habitation. Areas of the back beach near the sea, with only scattered ground vegetation and partially shaded by coconut palms, seemed most favored by both species. Female *S. signata* usually nested in moderate density ($\simeq$ 1 per m^2) toward the periphery of male flight areas. Female *B. variegata* nested in isolation or intermingled loosely with, and less densely among, female *S. signata.* Dense aggregations (> 15 per m^2) of *Microbembix monodonta* (Say) were also common.

Table 1. Descriptive statistics for burrows of *Stictia signata* and *Bicyrtes variegata* at Akumal, Quintana Roo, México.[a,b]

	Entry direction (degrees)			Distance from shore (m)			Slope down (degrees)[c]			Burrow length (cm)			Burrow depth (cm)		
Species	*n*	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE	*n*	$\bar{x}$	± SE
S. signata	16	157.6	18.1	17	41.1	2.5	12	32.5	2.4	13	32.9	2.9	12	21.2	1.2
							12	36.5	2.0						
B. variegata	24	149.2	8.5	24	30.8	2.8	23	36.3	1.8	24	13.1	0.7	24	9.0	0.5
							23	38.5	2.1						

[a] All measurements were not possible at all burrows; thus, sample sizes vary.

[b] Only included are burrows observed being provisioned or those that contained prey.

[c] Upper figures represent initial slope; lower, final slope.

Table 2. Numbers and taxa of nymphal hemipteran prey of *B. variegata* at Akumal, Quintana Roo, México.

	Family			
Cell	Alydidae	Coreidae	Pentatomidae	Scutelleridae
3a	1 (*Hyalemenus* sp.)	2	1	
3b		2		
5			5 (*Arvelius* sp.)	
6				1
7	1 (*Hyalemenus* sp.)		2	
9			2 (*Arvelius* sp.)	
12			3	
14			1	
17				2
18	2		1	1
21	1 (*Hyalemenus* sp.)		4	
37		1		
38			7	
40			1	
41			2	
42			1	
47			1 (*Arvelius* sp.)	
48			3 (*Arvelius* sp.)	
49		1	2	
52		7		
54		1 (*Leptoglossus* sp.)	1	
55	3 (*Hyalemenus* sp.)			
57	2 (*Hyalemenus* sp.)		1	
60			2 (*Arvelius* sp.)	
61				6 (Prob. *Homaemus* sp.)

Stictia signata *Female Activity.*—Females were observed digging during April, June–August, and December. December sightings were rare, but a large larva was recovered from an exhumed cell on 18 Dec 1984. During June, females dug or provisioned burrows as early as 05:20 h. Activity continued through early afternoon, slackened during mid-afternoon, then increased again, and tapered off after 17:00 h. Sand temperatures (taken on 14–15 Jun 1987 in sunny areas just below the surface of sand recently shaded by us) in wasp aggregations approximated 27° C at 06:00 h and 37° C from 10:00–14:00 h. Air temperature 7.6–15.2 cm above sand surfaces ranged from 28° C at 06:00 h to approximately 32° C from 10:15–14:00 h, and descended subsequently.

Burrow initiation usually began early in the day. Digging, closing, and leveling usually followed the descriptions of Evans (1966) for *Stictia carolina* (Fabr.). With few exceptions, possibly due to our disturbance, an outer closure was maintained even during regular provisioning of large larvae. Females arriving at nests frequently attracted small, possibly kleptoparasitic or scavenger dipterans that often succeeded in entering burrows with little reaction from the female wasps.

Entries to burrows usually were situated on the back beach in loose aggregations in compacted sand and averaged 41.1 m from the edge of the sea (Table 1). Burrows led toward the SSE (Table 1), in the general direction of the sea and into the prevailing direction of the wind. Burrows were longer than deep, and if multiply-pitched, they were slightly but not significantly ($P > 0.1$, Mann-Whitney *U*-test) steeper farther from the entrance (Table 1). Of 18 provisioned burrows that we excavated, all were unicellular with loose inner closures.

Provisioning involved dipteran prey, carried in the usual (see Evans 1966) position. Members of three families of Diptera were identified from exhumed cells (other taxa may have been represented in the fragmented material): Calliphoridae—*Chrysomya megacephala* (Fabr.) and *Cochliomyia macellaria* (Fabr.); Sarcophagidae—*Helicobia* sp. and three unidentified spp. of Sarcophaginae; Tachinidae—*Muscopteryx* sp. In addition to the wasp larva, small, probably scavenging or kleptoparasitic larvae occurred in most cells, and were usually buried in frass and loose sand.

Stictia signata *Male Activity.*—Sinuous, patrolling flight usually occurred approximately 0.5 m above the surface of extensive non-vegetated sandy areas. The flight was similar to that described for *S. carolina* by Evans (1966) and was conspicuous during most sunny mornings in April and from June through August. This activity usually began after 06:15 h, increased until 08:00–09:00 h, then slackened, and ceased between 10:30 and 12:00 h. Males frequently patrolled semi-exclusive, irregularly shaped areas of over 20 m^2. The sinuous flight patterns of males from adjoining patrol areas were occasionally interrupted by face-offs, head butting, and then upward flight by both males.

Stationary hovering also occurred in this population. At 07:00 h or usually later, males frequently appeared in hovering flight at relatively fixed positions. Hovering was not observed after 12:15 h. Hovering males were less common than those in patrolling flight. Males hovered in isolation or in groups; those in groups usually were dispersed horizontally and separated by at least 4 m. Individual hovering positions were held for as long as 1 h. Brief rests on nearby palm fronds and quick forays to interact with neighboring males occurred during hovering periods. Vertical stratification of hovering males also existed. In one situation (28 Jun 1986), five individuals hovered at various levels near shrubs—two spaced vertically between 1–1.6 m, and three spaced vertically between 2–4 m, while circuitous patrolling flight of other males occurred within 5 m. We observed hovering flight on 23 Apr 1986 and during June of 1985–1987, but made no attempt to define its seasonal limits beyond these dates.

Bicyrtes variegata *Female Behavior.*—Females were observed digging burrows during April, and from June through August, but not during December. Females became active later in the day than did *S. signata* females; their earliest digging was observed at 07:30 h (June) and earliest provisioning at 07:44 h (June). Digging involved accentuated body tilting. Stones up to 0.4 cm diameter occasionally were carried with the mandibles to the burrow entrance from inside and were tossed sideways away from it. Burrow initiation usually took place in the forenoon; completion took 45 min to 2.5+ h. Arriving females frequently attracted small, possibly kleptoparasitic or scavenging dipterans that frequently succeeded in entering the burrow. Female *B. variegata* exhibited only cursory or moderate negative reaction toward these flies.

After digging or provisioning, the wasps' exits from the burrow were usually head first. They maintained an outer closure of loose sand that was casually kicked inward or was more carefully constructed by entering the burrow backwards while kicking. Final abdominal tamping of the closure occurred in some instances. The wasps exited the site, after one to several orientation flights, in an upward departing flight.

Entries to *B. variegata* burrows were most frequently situated on the back beach in compacted sand, loosely scattered among *S. signata* burrows. Burrows led predominately toward the SSE, averaged 30.8 m from the sea, were longer than deep, and were not significantly ($P > 0.4$, Mann-Whitney *U*-test) steeper toward the rear (Table 1). Of 24 burrows exhumed, 23 had one cell and one had two cells. No inner closures were noted.

Provisioning with nymphal hemipterans occurred from 07:44 h to 17:04 h. Provisioning usually began on the same day as burrow initiation, and either was completed during that day, or extended to a second day. When wasps returned to burrows with prey, they descended by a vertical hovering flight. Wasps spent from 1–5 min inside the burrow during each provisioning visit; the shortest interprovisioning interval was 3 min, but provisioning intervals usually lasted 10–30+ min.

Four families of nymphal hemipterans were collected from 25 cells of 24 burrows between 8 Jun–5 Jul 1985; most were completely paralyzed. The wasp laid its egg in a semi-erect position on the mid-ventral line of the first hemipteran brought to the burrow, usually between the meso- and metacoxal bases. Pentatomids were used most frequently, followed by coreids, scutellerids and alydids (Table 2). Individuals of three families occurred in one cell, two families in six cells, and one in 18 cells (Table 2). In one cell, we found a quite large wasp larva 24 h after an adult had provisioned the burrow; in another, a large larva was found within one hour of a provisioning visit. This suggests that some progressive provisioning occurs in this species. A maximum of seven prey individuals was found in a cell (Table 2); this total, however, is biased by an early exhumation protocol but may be due in part to a scarcity of prey during drought conditions. In addition to the wasp larva, small, probably scavenging or kleptoparasitic larvae occurred in most cells.

The sizes of female *B. variegata* captured while digging varied considerably and may reflect resource shortage and foraging success. Dimensions of four specimens collected at Akumal ranged from 3.7–5.2 ($\bar{x} \pm$ SD: 4.3 ± 0.7) mm for head width, 12.3–19.2 (15.1 ± 3.2) mm for total length, and 9.5–14.0 (11.2 ± 2.1) mm for wing length.

Discussion

The digging behavior of female *S. signata* at Akumal was typical of that reported for the genus (Evans 1966). Burrow length was similar to that recorded for this species in Brazil (Post 1981), but shorter than that of other populations of *S. signata* (Evans 1966) or for other species of *Stictia* (Evans 1966, Evans & Matthews 1974, Matthews et al. 1981, Sheehan 1984).

Prey items of *S. signata* were from families of Diptera previously reported as utilized by this wasp (Evans 1966, Post 1981); *Cochliomyia macellaria* (Fabr.), taken for provisioning at Akumal, is also captured by *S. signata* on Dominica and Puerto Rico (Evans 1966) and in Brazil (Post 1981).

Females of *B. variegata* at Akumal are typical of those of other *Bicyrtes* (Evans 1966) in that they are only loosely (if at all) gregarious, and nested in isolation or among aggregations of another sand wasp. In contrast to the situation reported as typical by Evans (1966), burrows at Akumal were (one exception) unicellular; this characteristic and the considerable range of size of adults may reflect a patchy scarcity of prey occasioned by drought conditions in the area.

At Akumal, *B. variegata* utilized only immature hemipterans; Evans (1966) noted that adults were less common than nymphal stages among *Bicyrtes* prey. Also, as Evans (1966) summarized, pentatomids and coreids were the most common prey; however, nymphal alydids, not mentioned as prey of this genus by Evans (1966), nor by Evans & Matthews (1974), were also present.

Our observations of several concurrent intrademe flight patterns by male *S. signata* augment the alternative mating strategies reported for other sphecids (i.e., Alcock 1975, 1979; Evans & O'Neill 1978; O'Neill & Evans 1983a, b, 1988). Low, moving flight has been described for male *S. signata* in Quintana Roo by Evans (1966). Low hovering flight was reported by Post (1981) in Brazil. William Sheehan (personal communication) noted interpopulational differences in male *S. signata* flight at separate Costa Rican sites during different years: in one population, a low rapid directional patrol along a path in which females nested was seen; in another, males hovered within the spreading branches of a shrubby tree from near ground level to 4–5 m. Sheehan (personal communication) also observed alternative male flight patterns within populations of *Stictia heros* (Fabr.) in Costa Rica, where some males patrolled an open beach with fast low (10–20 cm) sinuous flight, while others held territories at the edge of the beach; individuals which were marked performed both behaviors.

Our data supplement those of studies that suggest that broad behavioral plasticity exists within sphecid species as an adaptive response to a variable environment (Alcock 1979, Alcock et al. 1978, O'Neill & Evans 1983b). We speculate that an unusual suite of attributes of *B. variegata* reported herein (reduced prey number, nymphal prey only, unicellular burrows, and small adult size) may reflect this adaptation and may have been mediated by a drought-influenced depauperate food chain.

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